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# A Re-evaluation of the Fromm's Landing Thylacine Tooth

By M. Archer*

Abstract: Reasons are given for considering that the Fromm's Landing thylacine tooth (A 57204) probably represents an individual conspecific with the modern *Thylacinus cynocephalus*. Certain dental abnormalities in thylacinid, dasyurid and macropodid teeth are considered. The functional significance of antcrolingual cusp development in some placental and marsupial tecth is discussed.

## INTRODUCTION

A small thylaeinc tooth (South Australian Museum No. A 57204) from an arehaeological excavation in a roek shelter at Fromm's Landing, South Australia, is describcd and illustratcd by Maeintosh and Mahoney, in an Appendix to Mulvaney, Lawton and Twidale (1964). Maeintosh and Mahoney coneluded that this tooth differed from the eighteen modern speeimens of *T. cynocephalus* available to them by its 'miniature size, bifid protocone, absenee of a definitive style $C_2$', and the 'presence of a minute style bueeally on the extremity of the metaeonal spur . . .'. They deeided that these differences 'when summated, prevent inclusion of the Fromm's Landing tooth in *T. cynocephalus*'. However, they also expressed the opinion that speeific determination would be premature because there was only one tooth.

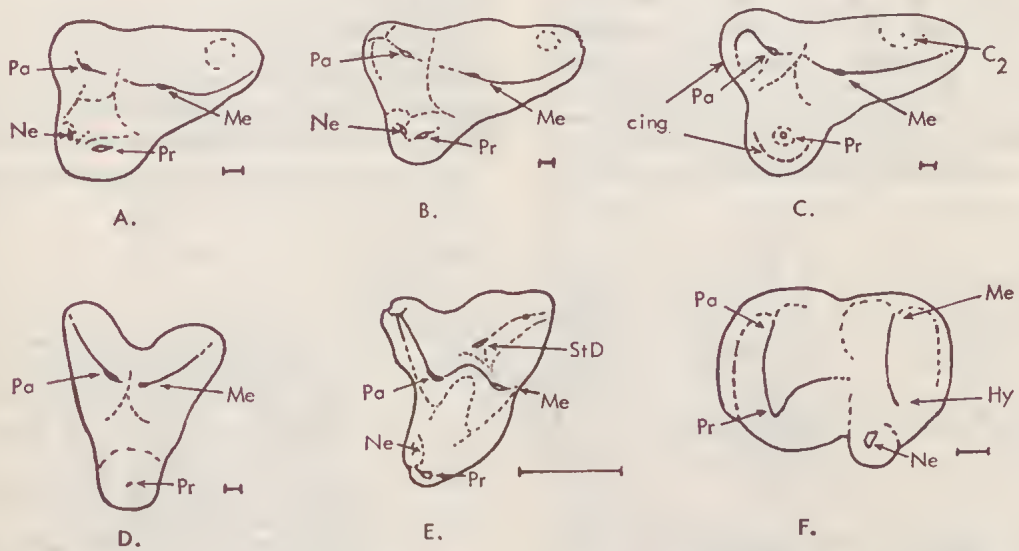


Fig. 1—Dental abnormalities in thylacine and other marsupial teeth. A. Fromm's Landing thylacine A 57204, $LM^1$ (adapted from Macintosh and Mahoney 1964); B. *Thylacinus cynocephalus* M 0138, $LM^1$; C. *Thylacinus* sp., Wellington Caves, N.S.W., $RM^1$ (reversed and shown as $LM^1$); D. *Thylacinus* sp., Wellington Caves, N.S.W., $RM^{4?}$; E. *Antechinus flavipes* M 8092, $LM^2$; F. *Macropus irma* M 6526, $LM^1$. Abbreviations: Pr = protocone; Pa = paracone; Me = metacone; Hy = hypoconc (topographic); Pcl = protoconulc; Mcl = mctaconulc; Ne = neomorphic cusp; StD = stylar cusp D (stylar cusp C of Slaughter 1968); $C_2$ = stylar cusp $C_2$ of Macintosh and Mahoney (1964) and originally of Bensley (1903); cing = cingulum; Plc = posterolingual cingulum. Each bar measure represents approximately onc millimetre in length.

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I have been able to examine this tooth (Fig. 1A) and conclude, for reasons set out below, that it can in fact represent an individual of the species *T. cynocephalus*. I use the dental symbolism of Ride (1964). All catalogue numbers unless otherwise noted are those of the Western Australian Museum Mammal Collection.

## THE DENTAL CHARACTERS

*The 'bifid protocone'*

I have examined the only two modern thylacine specimens, and all the fossil thylacine specimens available for study in the Western Australian Museum. Besides minor variations in dental morphology, I have observed in one modern thylacine (M 0138) the presence of a small anterolingual cusp on the flank of the protocone of the $LM^1$ and the $LM^2$, and the almost total absence of stylar cusp $C_2$ on the $LM^1$ (Fig. 1B). In one isolated thylacine $RM^1$ from the Wellington Cave deposits in New South Wales there is a distinct anterior cingulum (Fig. 1C). In another isolated $RM^{4?}$ (homology uncertain) from the same deposit there is an abnormal distribution of cusps (Fig. ID). Abnormalities in molar structure in other marsupials are not uncommon, particularly among phascogaline dasyurids. In a specimen of *Antechinus flavipes* (M 8092) which I bred in captivity, there is a distinct small anterolingual cusp on the $LM^2$ (Fig. 1E). In a specimen of *Sminthopsis macroura* (Queensland Museum specimen J 7407) there is a small cuspule developed on the anterolingual side of the $LM^1$ and $LM^2$. Similarly, one specimen of modern *Macropus irma* (M 6526) exhibits an extra cusp lingual to the topographic hypocone of the L and $RM^1$ (Fig. IF).

It is clear that abnormal lingual cusp development does occasionally occur in individuals of fossil and modern thylacinid populations, as well as individuals of various other marsupial groups. Similar supernumerary lingual cusp development occurs in placentals, as for example the Carabelli cusp in human dentitions. This has an incidence rate which evidently varies racially, but occurs among more than 40% of Caucasians (Van Reenen 1967).

*The 'definitive style, $C_2$'*

There is no cusp in this position on the $LM^1$ of the modern thylacine specimen M 0138 (Fig. 1B). However, there is a bulge on the crown in the area where the cusp would normally develop and where the cusp is developed on the $RM^1$ of the same specimen. There is a similar bulge on the Fromm's Landing tooth, although it is not as prominent.

*The 'small buccal style on the extremity of the metaconal spur'*

I do not consider that there is a significant cusp in this position on the Fromm's Landing tooth. If there is a swelling in this position, it is no better developed than it is in the modern thylacine specimen M 0138.

*The 'miniature size'*

Mrs. J. W. J. Lowry, who will shortly publish an analysis of certain small thylacines, has kindly supplied the following statement on the size of the Fromm's Landing thylacine tooth (A 57204):

I have compared my measurements of the Fromm's

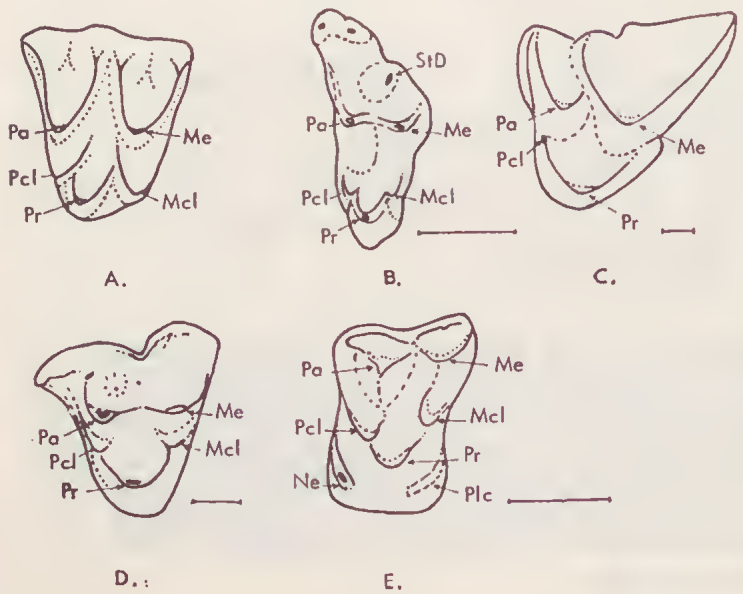


FIG. 2—Protoconule and neomorphic cusp development. A. *Desmana* (after Mills 1966); B. *Clemensia* (modified from Slaughter 1968, reversed and shown as a $LM^4$) $RM^4$; C. *Dasyurus maculatus* M 3855, $LM^3$; D. *Alphadon* (modified from Clemens 1966) $LM^2$; E. *Nyctitherium* (modified from McKenna 1960, reversed and shown as a $LM^2$) $RM^2$. Abbreviations as in Fig. 1. Each bar measure represents approximately one millimetre in length.

Landing thylacine tooth with the dimensions of the $M^1$s from the remains of 7 thylacines from caves in the Eucla Division of Western Australia (Lowry and Lowry, 1967; Partridge, 1967), and conclude that its length is contained in the range of lengths observed in the Eucla Division sample. Mean dimensions of dental characters from this Eucla Division sample are smaller than those of a sample of thylacine remains from caves in the southwest of Western Australia, but in most characters the difference is not statistically significant at the 5 per cent level. Ride (1964) considered that his southwestern sample, although statistically significantly smaller than modern *Thylacinus cynocephalus* in many characters, did not represent a separate species of *Thylacinus*. The remains considered here are believed to be all Recent to late Pleistocene in age (Merrilees, 1968), and there is no good reason to believe that they do not represent a single species that was more variable in the past. Thus the marked smallness of the Fromm's Landing thylacine tooth does not seem to be sufficient reason alone to separate it from *T. cynocephalus*.

## DISCUSSION

The Fromm's Landing tooth, from a level dated at approximately 4,000 years BP (Macintosh and Mahoney 1964) may represent the extant species *T. cynocephalus*, or some other valid species now extinct. Several species of *Thylacinus* have been described, namely *T. cynocephalus*, *T. spelaeus*, *T. rostralis* and *T. potens*. Only the first three of these are accepted as being Quaternary in age. Ride (1964) analysed characters of Pleistocene and Recent thylacines and concluded that there is no statistical basis for the separation of *T. cynocephalus* and *T. spelaeus* into more than one species. However, Ride pointed out that the measurements of some specimens from Darling Downs and New Guinea may indicate the presence of one or more additional species and suggested that the Darling Downs specimens may represent the characters of *T. rostralis* De Vis. Van Deusen (1963) comments on the New Guinea thylacine specimen but does not suggest that it necessarily represents an undescribed species.

J. Lowry has suggested (above) that the small size of the Fromm's Landing tooth seems insufficient reason to conclude that it does not represent *T. cynocephalus*, and I have shown above that the three remaining characters discussed by Macintosh and Mahoney (1964) are not unique to the Fromm's Landing tooth but are features also of the modern thylacine specimen M 0138. However, since I have seen no specimen of any thylacine species in which the 'bifid protocone' is as distinct as it is in the Fromm's Landing tooth, this may be a character which could be distinguished as representative of a separate species. There are thus two reasonable interpretations of this structure: 1. It is in fact an abnormality of dubious or minimal taxonomic significance such as are the structural abnormalities noted above in molars of other species or; 2. It represents a significant development characteristic of an extinct population of thylacines. We will consider both alternatives.

If the cusp is a significant functional and characteristic feature of a species of *Thylacinus* we may be able to determine what this function may have been by considering lingual cusp development in other species. Enlargement of the metaconule has been a feature of marsupial evolution, as for example in the perameline peramelids, glasbiine didelphids and probably the marsupial diprotodont herbivores. In these forms, the cusp I interpret as the enlarged metaconule functions as a topographic hypocone analogous with the polyphyletic hypocones of various placentals. Enlargement of a topographic anterolingual protoconule is not uncommon among placental insectivores such as *Desmana* (Fig. 2A) but a significant enlargement of this cusp is virtually unknown among marsupials, although it is present in such Cretaceous forms as *Clemensia* (Fig. 2B), *Alphadon* (Fig. 2D) and other didelphine didelphids. It is miniscule in most dasyurids (Fig. 2C) and peramelids. In addition to protoconule development, there are some instances of neomorphic anterolingual cusp development in placentals, such as in one specimen of a species of the Eocene genus *Nyctitherium* (Fig. 2E). Here the neomorph clearly has nothing to do with the well-developed topographic protoconule. Although I suspect that the anterolingual cusp in the Fromm's Landing tooth is a protoconule, the question of homology is less significant than that of function. The cusp may as well be considered a neomorph as is surely the case in the specimen of the species of *Nyctitherium*. Mills (1966) suggests that certain minor cuspules such as the protoconule and mesostyle may act as stops at the end of grooves to prevent spillage of food. This is presumably one function of the protoconule in *Desmana* and possibly in the Cretaceous didelphoids. Such a protoconule that confines food would be a useful feature in dentitions that are wholly or partly adapted for pulverizing. The food particles are maintained on an occlusal crushing surface for a greater amount of the time involved in mastication than they are in a dentition adapted largely for vertical shearing. In shearing the emphasis is placed on efficient slicing of tough or resilient food. Talon development restricts the depth or amount of the vertical shear by producing an impediment against which the talonid occludes. For example, the absence of talonid or

conule development in the marsupial mole *Notoryctes* results in almost unlimited vertical shearing potential, whereas the production of topographic hypocones and anterolingual cusps commonly reduces the amount of vertical shear. In extreme conditions such as in hominids (Crompton and Hiiemae 1969) and vombatids vertical molar shear is virtually eliminated. In the species of *Nyctitherium* exhibiting anterolingual cusp development the neomorphic cusp would probably restrict vertical shear, but because of its low and peripheral position on the crown may not have acted as a 'stop' as does the protoconule of *Desmana*. Rather, it might have served a double function by providing a ramp for the lower molar after it approaches centric position to help initiate the lingual phase of chewing, as well as by providing a lateral shear surface with a corresponding portion of the lower molar. In the modern thylacine specimen M 1038 the anterolingual cusp does not clearly serve any of these functions. It is not at the end of a groove to act as a stop, nor is it large enough to affect the trigonid or provide a lateral shearing surface. It is perhaps more appropriately considered as an anterior bulge on the protocone. On the other hand, the anterolingual cusp of the Fromm's Landing tooth is considerably larger and could act as a confining structure around the small protoconal basin. It probably did not affect the trigonid because of its proximal position to the protoconal basin and its small size compared with the neomorphic cusp of the specimen of the species of *Nyctitherium*. The tip of this cusp exhibits wear, but because it is the same type of coarse wear pattern exhibited by the major trigon cusps I would conclude that this was wear due to the abrasion of food particles rather than to occlusion. The cusp does not therefore appear to provide a lateral shearing surface.

In favour of the other alternative, that the cusp is an abnormality of minimal or dubious taxonomic significance, is the evidence presented above for the clearly abnormal appearance of a similar cusp in a modern specimen of the dasyurid species *Antechinus flavipes*, and the abnormal appearance of a similar but less developed neomorphic cusp in a specimen of the modern *Thylacinus cynocephalus*. Further evidence for the suggestion that it is an abnormality is provided by Kurten (1967) who demonstrated that in samples of fossil ursid populations from caves, dental variation was higher in juvenile skulls than it was in adult skulls. He interpreted this as evidence for selection against certain dental variation. The Fromm's Landing tooth does not represent an old individual. Similarly, the abnormal modern thylacine is a young animal with the $M^3$ just erupting.

Finally, it is worth considering that one of the major characteristics of the thylacinids is their protocone-talonid reduction and consequent development of long and high shearing crests. Since it is reasonable to assume that this is a derived condition from a more generalized didelphoid (or possibly dasyurid) condition, it would mean that if the anterolingual cusp under discussion is a development with adaptive significance, some thylacinids are now (M 0138) and have been (Fromm's Landing tooth) undergoing a reversal of this trend and producing a more significant talon-talonid development. It is perhaps curious that if this is so, it should be so comparatively rare in modern thylacines. It is also curious that no other fossil thylacine specimens known to me, from the Nullarbor or south-west or south-east Australia, which probably bracket the age of the Fromm's Landing tooth, exhibit this character. However the possibility that it is not an abnormality cannot be discounted on this evidence alone.

## CONCLUSIONS

It is most probable that the Fromm's Landing thylacine molar represents an individual conspecific with the modern *Thylacinus cynocephalus*.

This conclusion is based on the fact that the structures it presents are not unique and are represented in part as abnormalities in a modern thylacine specimen and also in one character by a specimen of the dasyurid species *Antechinus flavipes*. It is conceivable, however, that the presence of the anterolingual neomorphic cusp in the Fromm's Landing tooth is characteristic of an as yet unknown thylacine population. The cusp could be functional and hence adaptive. The possibility cannot be discounted on the basis of negative evidence or improbability. On the other hand, there is positive evidence to suggest that the cusp is an abnormality in *T. cynocephalus* (as in M 0138) and hence the Fromm's Landing tooth should not be considered to differ significantly from the modern species on the basis of this character.

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